Vocal Competition

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Corresponding Author	Family Name	**Castellano**
	Particle	
	Given Name	**Sergio**
	Suffix	
	Organization/University	University of Turin AU1
	City	Turin
	Country	Italy
	Email	sergio.castellano@unito.it
	Email	scastell@unito.it

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Vocal Competition

Sergio Castellano
University of Turin, Turin, Italy

Synonyms

Acoustic competition

Definition

Agonistic interactions mediated by the production of acoustic signals

Introduction

It is late autumn in the temperate forest, the last leaves still on the trees finally surrender to the northern breeze and fall down, silently. The beams, as the sun sinks, pass through the naked branches and illuminate the forest clearing, where a large, old stag is moving restlessly around a group of quietly foraging females. Not far away, a young solitary male observes the scene. The breeding season is almost over and the young male has not yet mated. Testosterone, flowing abundant in his blood, makes him decide to challenge the rival, in the attempt of conquering his harem. As he moves a few meters ahead, the rival spots him and, suddenly, stops, raises the head, opens the mouth, and starts uttering grave, loud roars. The young responds in the same way. A vocal competition has begun.

Vocal competitions are common in many arthropods and vertebrates, which are the only taxa that evolved the ability to communicate by means of sounds (Bradbury and Vehrencamp 2011). Acoustic signals are well adapted to mediate agonistic conflicts. Since sounds are effective on the long distance, they prevent physical contacts and reduce the risk of uncontrolled fighting escalations. Sounds are under strong morphophysiological constraints and are thus preadapted to encode reliable information about the sender's fighting ability. Sound modulation further increases the communicative potential of acoustic signals, and it allows to flexibly adjust signals to the unpredictable dynamics of the ongoing competitions.

Vocal competition can be direct or indirect. In the following paragraphs, we shall consider the effects of these two mechanisms on the evolution of agonistic signals.

Vocal Contests

The vocal contest, such as that described in the red deer, is a mechanism of direct vocal competition. Two conflicting individuals exchange agonistic signals in order to resolve conflict to their own advantage. In this communicative interaction, the actors play both the sender and the receiver role.

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Since the degree of conflicting interest between senders and receivers is high, agonistic signals can be evolutionarily stable only if they provide receivers with honest information about the fighting ability and the aggressive motivation of the sender (Bradbury and Vehrencamp 2011). Natural selection can guarantee the honesty of agonistic signals by imposing either strategic costs or morphophysiological constraints on their expression (Maynard Smith and Harper 2003). The roar of the red deer is a good example of both solutions. In fact, fighting ability depends on body size and stamina (the ability to sustain prolonged energetically costly activities), and the roars of the red deer convey honest information of both these traits. When roaring, the stag retracts the mobile larynx down to the sternum (Reby and McComb 2003). The sound produced by the vibrating vocal folds resonates into the vocal tube; some frequencies are filtered out, whereas others, the formants, are amplified. The frequency of the lowest formant is strongly and negatively correlated with the length and volume of the vocal tube and, thus, with the male body size. Playback experiments have shown that the roar spectral properties affect the contest outcome, favoring the individuals with the lowest formants. Independent of body size, the fighting ability of a male depends also on how much energy stores he has and on how good he is in using the energy in controlling aerobic and anaerobic metabolic rates. In the red deer, roaring is energetically costly and involves muscles that are important during fighting. The high strategic costs of sustained vocal contests, thus, is a reliable indicator of male fighting ability.

Vocal contests are common in most acoustic-communicating species. For example, in the house cricket, *Acheta domestica*, male-male aggressive interactions typically begun with the production of stridulatory calls, which differ from mate-attraction calls in both spectral and temporal structures. In this case, honest information of male body size is encoded in the temporal properties (the number and the rate of pulses within a call), rather than in the frequency components of the call (Greenfield 2002). In territorial songbirds, vocal contests are often a mechanism for resolving boundary disputes. During the contest, birds of neighboring territories interact acoustically on a short time scale in order to assess reciprocal differences in motivation and to establish relative dominance. The dawn chorus of many territorial songbirds is an unusual example of vocal context, because it does not involve dyadic interactions between conflicting individuals. With their vigorous signaling, territorial males communicate their presence and condition to prevent rather than to prevail over potential rivals.

Indirect Vocal Competition

Unlike in vocal contests, in indirect competitions, the outcome of agonistic interactions depends on the behavior of a third-party actor, who plays the receiver role. A typical example is represented by lek breeding species, where males aggregate in large choruses and compete acoustically against each other to attract gravid females. In this case, selection promotes the evolution of acoustic traits, which might be poor indicators of fighting ability, but good indicators of sexual attractiveness. Mate choice theories of sexual selection try to understand the functional significance of mate attractiveness.

The distinction between direct and indirect vocal competition, however, is not always clear cut. In many species, in fact, the same acoustic signal may be used in both direct and indirect competition. For example, in the red deer, the acoustic properties that are important for solving intra-sexual agonistic interactions are also those perceived as most attractive by females. In contrast, in other species, direct and indirect vocal competitions conflict with each other. For example, in tree frogs and toads, males often compete for display positions within the chorus. During these agonistic interactions, males have been observed to reduce the dominant frequency of their advertisement calls, and playback experiments showed that the greater the reduction, the more effective the call was in repelling the opponent (Gerhardt and Huber 2002). Frogs and toads, however, have a poor control over the resonant frequency of their vocal folds, and the only way they have to reduce the frequency is by reducing

the vibrating pressure of vocal folds, with a consequent reduction in call intensity. The intensity reduction may have no effect on the short distances at which male-male interactions occur, but it may have strong negative effects on the long distances, where male-female interactions occur. In this case, selection is expected to promote the evolution of optimal tradeoffs between the conflicting functions.

Indirect Vocal Competition in "Selfish" Choruses

Indirect vocal competition arises because signaling males tend to aggregate in spatially restricted areas. In some cases, aggregation can be explained by the inhomogeneous distribution of the limiting resources. For example, male frogs aggregate at the breeding ponds, because here is where females lay their eggs. In other cases, however, aggregation may be favored by natural selection, because the benefits it provides overcome the competition costs it imposes. This happens when group size shows either a positive allometry with the number of visiting females or a negative allometry with the number of visiting predators, or both. Whatever the reason, aggregation adds a new level of competition in the population, because males not only compete against their rivals within a chorus but, as members of a chorus, they also compete against the members of other choruses within a network. The two levels of vocal competition may interact and affect the spatial and the temporal structure of vocal activities.

Vocal competition within a chorus can cause signalers to couple their calling to that of their rivals. Coupling may occur both at the gross and at the fine temporal scale. At the gross-scale level, it usually results in synchronous calling. For example, tree frogs alternate prolonged bouts of calling with periods of silence, and they do this synchronously within a chorus. In this way, tree frogs may reduce the risk of being predated by passive listening predators, such as bats (i.e., an "acoustic dilution effect"), and, at the same time, they may increase the power of the overall signal to attract females from further away (Gerhardt and Huber 2002). In contrast, at the fine-scale level, coupling results more often in alternate than in synchronous patterns, at least in those species where the fine-scale structure of the call conveys important information for species recognition. Alternation might be interpreted as a form of "selfish" signaler cooperation, because chorusing males share the same common interest of making their own signals as detectable as possible. Males that fail to alternate would reduce their own mating success and, incidentally, that of their neighbors. Alternation can also arise as a side effect of male-male vocal competition. In many species of frogs and insects, in fact, females show strong preferences for the male that call first (acoustic leader) (Gerhardt and Huber 2002). Males can thus compete against their closest neighbors for temporal primacy and this would result in regular antiphonal calling.

Vocal Competition in Cooperative Choruses

So far we have considered vocal competition of selfish choruses. However, in some birds and mammals with a solid social organization, vocal competition often occurs between social groups, and, at the within-group level, individuals cooperate to improve the overall calling performance (Ravignani et al. 2014). In many tropical bird species, the members of a pair are known to coordinate their songs, by accurately alternating their components. In some species, the social group includes helpers, who join to produce a complex chorus, in which individuals of the same sex sing the same phrases with near-perfect synchrony (Mann et al. 2006). Chorusing behavior in birds is thought to solve two main functions: it favors coordination among the members of a group and it improves vocal contest performances in mutual territorial defense. In primates, chorusing (mostly in the form of duetting) has been observed in a few genera only. A well-studied example is that of the singing lemur, *Indris indris* (Gamba et al. 2016). In this species, all members of a group usually sing, but the contribution changes in relation to the social rank, suggesting that chorusing

not only solves the function of communicating group size and cohesiveness during the vocal contexts with neighboring groups but it may also play a role in mediating within-group social conflicts.

Conclusions

Direct and indirect mechanisms of vocal competition have favored the evolution of signals that are a reliable indicators of signalers' competitive quality (fighting ability or attractiveness). Morphophysiological constraints preadapted some sound properties to this function. But evolutionary stability is most likely the consequence of the strategic costs of cheating: the risk of fighting escalation in vocal contests and the energetic costs of sustained calling in choruses make the bluff an economically disadvantageous tactic.

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